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Some Ecological Factors in Secondary Succession: Upland Hardwood

I. Evaporation Studies in the Sycamore Creek Region

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SOME ECOLOGICAL FACTORS IN SECONDARY SUCCESSION: UPLAND HARDWOOD

I. EVAPORATION STUDIES IN THE SYCAMORE CREEK REGION

By Stanley A. Cain *and* Ray C. Friesner

The central hardwood region has been divided by the foresters into the "upland type" and the "bottom-land type." Tillotson (7). Under the upland type there is a subtype, "mixed hardwoods and conifers." The upland type includes the areas with higher, well-drained soils; the bottom-land type is characteristic of the moister, slower drained soils. From an ecological point of view, there are a number of natural vegetational groups which represent successional stages leading up to the widespread Beech-maple climax. The later stages in both the xerophytic and hydrophytic succession are dominated by certain tree species. The exact species of these groups and the relative duration of the successive stages are influenced, of course, by many factors, floristic, topographic, edaphic and climatic, variable over the region.

In the climax condition this widespread Beech-maple formation is varied by the addition of hemlock on the north and northeast, and in the south by the admixture of magnolia and live oak. On the west the beech gradually drops out, as later does the maple, leaving the oaks to form the climax woodland and the parklike prairie-woodland transition, known as savannah.

The present stands of timber in this extensive central hardwood region are about three-fourths in farm woodlots of relatively small extent, representing the culled remnants of what was a most magnificent and essentially unbroken hardwood forest. As a very large part of these wood-producing areas are in a decadent condition as a result of fire, over-grazing and an ignorance of silvicultural methods, it would seem that the greater portion of the timber is on the sure march to extinction. This extensive situation, coupled with the fact there is an untold acreage of wornout and abandoned farm land in the poorer hilly sections of Kentucky, Ohio and Indiana gradually reverting to forest cover, warrants a study of any of the factors which are related to the situation. Who can tell what may be the demand in the future upon a knowledge of the climatic and edaphic factors related to this natural

reforestation? The problem of these areas and their wood crop must, inevitably, in no distanct future, become more acute.

In the regions of the lowland type of forest the soils are usually more fertile and generally better suited to permanent agricultural cropping than they are in the hilly upland regions. So it is in the latter where the foresters hope to develop the "timber crop" idea. The lowland type is marked by such "key" species as red gum, cottonwood, river birch, cypress, willow oak, sycamore, willow, silver maple, overcup oak, swamp white oak, etc. Other species to be considered as common or as occasional are slippery elm, pin oak, black ash, yellow poplar, white oak, sugar maple, black cherry, blue ash, honey locust, northern red oak, butternut, buckeye, etc. The upland type is characterized less by key species than by their absence. Trees of the upland type to be considered "distinctive" include chestnut, chestnut oak, pignut, hickory, post oak, blackjack oak and the like. Under more mesophtic conditions the upland forest includes beech and maple, basswood, white ash, white oak, green ash, black walnut, yellow poplar, black cherry, etc. The conifer-hardwood subtype includes juniper in many places, short-leaf pine in the Ozarks, and Virginia scrub pine in the knobs of southern Indiana and Ohio, mixed with hardwoods, largely oaks.

In the Knobs region of south central Indiana, which is the unglaciated portion of the state, the existing woodlands are largely of the oak-hickory type. Very little virgin timber remains or even well-cared-for stands of any age; the stands are mostly second-growth or severely culled remnants from which the more valuable tree species have been practically eliminated. The ordinary small landowners in these regions are usually so hard-pressed economically that they cut every stick when it reaches merchantable size. However, under wise silvicultural practice, a perpetual forest crop could be produced to meet the steady demands for ties, mine props and the like; but in most places the valuable tree species are being eliminated and worthless "weed" species, such as ironwood, blue beech, dogwood, blackjack oak, persimmon, sassafras, redbud, post oak, etc., are gaining in percentage. See Tillotson (7). Yet timber is a persistent crop, and, if given a chance by protection from fire, over-grazing and unwise cutting, the more desirable species will return in steadily higher percentages.

A statistical floristic study of second-growth hardwood is in process, but, *ad interim,* a brief description is necessary of the region where the

present data on evaporation and the material on soil acidity, to be presented in Paper 2, was obtained.

Description of Atmometer Stations—Five evaporation stations were located in the Sycamore Creek hill region and were maintained from May 12 to September 29, an elapse of twenty weeks. This run of data practically covers the frost-free period. As a matter of fact, the last week's readings are incomplete as a result of frost damage to some of the atmometer bulbs.

The five stations were indicated as follows:

Station A—Beech-maple climax.

Station B—Sassafras-aspen-sumach thicket.

Station C—Blackberry-cinquefoil old-field association.

Station D—Mesophytic ravine.

Station E—Oak ridge association.

Of these five stations, the results in C, B and E are most important and interesting, since these stations were in comparable topographic situations and also represent normal stages vegetationally in the reforestation of deforested land in this region.

Numerous lateral tributaries to the main stream have resulted in a number of more or less parallel ridges and ravines. These terminate abruptly in the main stream, the ridges ending in sheer bluffs of bare rock. The whole region has been cut over a number of times by small portable mills, taking out all the trees large enough for cross-ties. The ravines recover quickly but with a large percentage of worthless species. The ridges are more severely damaged and are consequently recovering more slowly. Many of these ridges have been burned over after cutting, a damage most of the ravines have not suffered because of their greater protection and moisture. Some of the ridges have been cleared for pasturage or cropping, but have practically all been found unsuitable for agriculture and are now in various stages of reforestation. This natural secondary succession is extremely slow and many valuable tree species are not coming back in their former abundance.

Atmometer Station C is located on one of these narrow ridges near where it terminates in a rock bluff about a hundred feet high. This ridge has been cut over and burned, after which it was probably pastured. It has now been abandoned for a few years and is occupied by the following plants: The most abundant woody plants are *Rubus allegheniensis,*[1]

[1]Nomenclature: Gray's New Manual of Botany, 7th Ed.

Vaccinium vacillans, Gaylussacia baccata, which may be considered dominant in the shrub layer. Dominant in the herb layer are *Poa compressa,* an unidentified *Carex* species, and *Potentilla canadensis.* Numerous and extensive moss and lichen colonies form the soil cover. Conspicuous here are the following: *Polytrichum juniperinum, Catherinea angustata, Leucobryum glaucum, Dicranum scoparium, Dicranella heteromalla, Funaria hygrometrica, Cladonia coccifera, Cladonia rangiferina,* etc. The sides of the ridge are more or less occupied by various trees. Some of the species that are working their way into this old-field are: *Populus grandidentata, Rhus glabra, Sassafras variifolium* and *Carya ovata.*

Atmometer Station B is located on another ridge top. The slope to the north leads down to the creek, while a parallel ravine bounds the ridge on the south. The north slope is occupied by a Beech-maple climax, to be described later, since Station A is located in it. The ravine on the south is occupied by an oak association. The ridge itself is grown up in a thicket of old-field species, namely, *Populus grandidentata, Sassafras variifolium, Rhus glabra,* which range up to twenty or thirty feet high. Some of the characteristic plants of this community are: *Potentilla canadensis, Viola triloba, Arabis laevigata, Ribes cynosbati, Rubus allegheniensis, Krigia amplexicalis, Liparis lilliifolium* and *Ophioglossum vulgatum.*

Atmometer Station E is back quite a distance from Sycamore Creek but is on a narrow east-west ridge, as were Stations C and B. This ridge is occupied by an oak association. It is made up largely of second-growth oak and probably represents the culled remnants of the former woodland. It is maintained, however, that this oak association is essentially the same as would be developed by natural reforestation of old-fields. That it is not at present in the climax stage is shown by the luxurience of undershrub growth.

It was not possible to locate with certainty an old-field which had developed so far in the secondary succession, since a great elapse of time is required for an old-field to reach the oak stage. Among the species which give character to the woods are *Quercus rubra, Q. alba, Q. velutina, Q. muhlenbergii, Carya ovata* and *Liriodendron tulipifera.*

Two other groups of species are of interest. One group, including *Sassafras variifolium, Nyssa sylvatica, Acer rubrum* and *Populus grandidentata,* are indicative of this ridge having once been at least clear-cut if not an old-field. Certain other species indicate, either, some

advance beyond the typical oak association, or, that the present oak dominance is a result of the method of cutting which has eliminated most species of the more advanced stage, of which the following are remnants: *Prunus serotina, Fagus grandifolia, Morus rubra, Ostrya virginiana, Cornus florida, Fraxinus lanceolata* and *Acer saccharum.* The possible significance of these two groups is merely suggested. To know which is correct would demand a longer acquaintance with the region. Other species of interest are: *Ampelopsis quinquefolia, Rhus toxicodendon, Galium lanceolatum, Podophyllum peltatum, Viola triloba, Erythronium americanum, Eupatorium urticaefolium, Krigia amplexicaulis, Arisaema triphyllum, Geum vernum, Smilacina racemosa,* and the ferns *Botrychium virginianum, Aspidium noveboracense* and *Polystichum acrostichoides.*

Atmometer Station A is situated about halfway up a steep slope bordering Sycamore Creek. This station is in a Beech-maple climax association and has a northern exposure. It is assumed in this case also that the conditions in this Beech-maple climax are the same as they would be if the association were the culmination of the stages in secondary succession on a deforested area. When these atmometer stations were set up in the spring of 1928, no ridge physiographically similar to those on which C, B and E were located was known which had the Beech-maple climax. It is recognized that Station A is not comparable topographically and that the evaporation results are consequently to be viewed in the light of this fact. Over sixty species were observed in the vicinity of this station. *Fagus grandifolia* and *Acer saccharum* are the dominant trees. Other trees and shrubs in this community are: *Prunus serotina, Acer rubrum, Quercus alba, Cornus florida, Ostrya virginiana, Carpinus caroliniana, Hamamelis virginiana, Ulmus americana, Hydrangea arborescens, Viburnum acerifolium,* etc.

The herbaceous flora is decidedly vernal in its aspect, including the following: *Stylophorum diphyllum, Podophyllum peltatum, Geranium maculatum, Erythronium americanum, Claytonia virginica, Dentaria laciniata, Mitella diphylla, Sanguinaria canadensis, Anemonella thalictroides, Hydrophyllum appendiculatum,* etc.

Station D was located in a narrow, V-shaped ravine, where the topography offered a maximum of protection. The ravine is from thirty to forty feet deep and bends sharply just above and below the location of the station. The sides of the ravine are so steep that the soil is only held in place by the richness of the vegetational covering. This station

bears no relation to the second-growth hardwood succession represented in Stations C, B, E and A, but was established to show the effect of topography.

Common herbs in the vicinity of Station D are *Phacelia bipinnatifida, Mitella diphylla, Silene virginica, Asarum canadense acuminatum, Hepatica acutiloba, Polygonatum commutatum, Dicentra cucullaria,* etc.

PROCEDURE—Porous porcelain spherical atmometers [manufactured by Dr. Burton E. Livingston (6), 6214 Oak Lane, Cedarcroft, Baltimore, Md.] were used throughout these experiments. Atmometers were operated in pairs at all stations. The behavior of these instruments was checked by running a third atmometer at a station where there was any sign of irregularity. Each atmometer was mounted on a reservoir bottle containing about 400 cc of distilled water. The delivery tube was projected well into the bulb and extended downward through the rubber stoppers to the bottom of the reservoir. In each delivery tub a rain-proof valve was constructed. This valve is simple in construction. It consists of a globule of mercury about twice the diameter of the bore of the delivery tube, which is held in place by plugs of cotton or sheep's wool. Penetrating the stopper of the reservoir bottle are two short glass tubes, both of which extend above the top of the stopper about three-fourths of an inch. They are loosely capped by small vials which keep out the rain but are not air-tight. One tube is flush with the bottom of the stopper while the other extends about two inches into the reservoir. The latter tube is for refilling the reservoir, while the former acts as an air vent. It was found that the reservoirs were best refilled by use of a small funnel hooked up with the glass tube by a short piece of rubber tubing. The distilled water required to refill the reservoir each time was measured by use of a 100 cc graduate. When readings are taken by weekly periods there is no need for using a pipette, as the method described is sufficiently accurate. This system of filling the bottles seems to be better than one requiring the removal of the stoppers.

The atmometers were fixed in flowerpots which were sunk in the ground so that the bulbs were held securely erect at a constant height of about eight inches above the ground. As has been shown by Fuller, Livingston and others, this region is the most significant one, since it is the zone where the seedlings must establish themselves. When the two atmometers at any one station were found to differ in rate of

water loss, they were checked by the addition of a third atmometer, or by the reversal of position of the two atmometers at the station. As a result of the latter procedure, it was discovered that two atmometers one meter apart may show consistent differences in the rate of water loss.

Results and Procedure—To the ecologist the evaporating power of the air represents the summation of the various atmospheric factors: temperature, humidity, air movement and insolation. These factors can be measured separately, of course, and each effects water loss from the plant. However, the evaporating power of the air, as measured by the Livingston porous clay atmometer, is a summation of all these factors, and so becomes the best single measure of the atmospheric conditions for plant growth. When evaporation is expressed in terms of daily or weekly loss for seasonal periods, and is related to vegetation, it is found to be one of the most vital factors of the habitat. Livingston (4) (5) plotted a map of weekly evaporation rates for the United States and came to the following conclusions: "(a) Regions with similar evaporation have similar vegetation; (b) evaporation power of the air is the most important factor in plant distribution." In a general way, then, evaporation regions and climatic plant formations are found to be correlated.

As early as 1908, Transeau (8) measured the evaporating power of the air in several plant associations near Cold Spring Harbor, L. I. Fuller (2) gave the first records of evaporation which extended throughout a growing season. His stations were continued through three seasons and the data were presented along with findings on the growth water of the soil. He makes an intimate connection between vaporation rates and the succession of plant associations which is substantiated by Weaver (9). The rate of evaporation is higher in pioneer associations and lower in the climax associations. Gleason and Gates (3) also observed this relation, but thought that the differences in vegetation caused the differences in evaporation. Fuller maintains, with indisputable evidence, that evaporation is a factor in the succession. A change in habitat leads to a change in vegetation. So far as the writers are aware, a study of evaporation rates has not been applied to the plant associations in secondary succession, upland hardwood, so it was with this in mind that the Sycamore Creek project was taken up.

A sample table of the data obtained by weekly periods for these stations is given as Table I. The standardized results of the whole season's

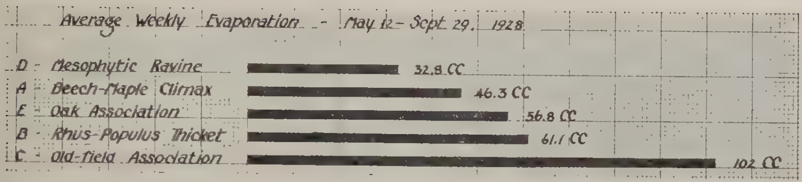
work is condensed into Table II. It was not found feasible to present graphic representation of this data except for Fig. 1, which presents the average weekly loss by stations for the twenty-weeks season.

TABLE I, EVAPORATION DATA FOR THE WEEK, MAY 12-19, 1928

Station	Succession Type	Atmometer	Loss cc	Standardized	Average
C	(1) Old field	S 28-87	203	160.37	
	" "	S 28-91	192	151.68	156 cc
B	(2) Thicket	S 28-94	175	138.25	
	"	S 28-119	168	132.72	135 cc
E	(3) Oak woods	S 28-115	165	131.25	
	" "	S 28-95	173	136.67	134 cc
A	(4) Beech woods	S 28-102	129	101.91	
	" "	S 28-113	126	99.54	100 cc
D	Wooded ravine	S 28-82	147	116.13	
	" "	S 28-84	143	112.97	114 cc

TABLE II, STANDARD AVERAGE EVAPORATION IN cc, May 12 - Sept. 29, 1928

Week ending	Station					Average	Season
	C	B	E	A	D		
5/19	156	135	134	100	114	127.8	Spring av.
5/26	141	125	121	98	86	114.2	121
6/2	98	78	62	58	48	68.8	
6/9	56	—	48	32	22	39.5	
6/16	117	55	74	62	52	72.0	Early summer
6/23	59	40	26	36	12	34.6	av. 48.8
6/30	56	34	22	20	14	29.2	
7/7	90	56	38	38	20	48.0	
7/14	96	63	43	37	25	53.6	
7/21	100	60	39	37	21	51.4	
7/28	96	60	40	45	23	52.8	
8/4	108	69	49	38	24	57.6	
8/11	98	45	30	25	16	42.8	Mid summer
8/18	112	64	56	42	29	60.6	av. 51.5
8/25	94	44	41	31	19	45.8	
9/1	101	29	38	27	13	41.6	
9/8	115	30	56	51	24	55.2	
9/15	119	45	61	30	13	53.6	Early autumn
9/22	126	89	84	—	35	83.5	av. 57.6
9/29	—	40	66	74	36	54.0	
Total	1938	1161	1136	881	656		
Weekly	102	61.1	56.8	46.3	32.8		
Daily	14.6	8.7	8.1	6.6	4.7		



It is of some interest to compare these results with those of other workers. Fuller (2) selected the climax Beech-maple forest as a standard upon which to base comparative rates of evaporation for different plant associations. This he represented as 100, on which basis the various associations compared, over a three-season period, as follows:

Cottonwood dune	319
Pine dune	149
Oak dune	157
Oak-hickory forest	126
Beech-maple forest	100
Prairie (Edaphic)	179

Our results for one season, with the Beech-maple forest also as unity, compare thus:

Old-field (Station C)	220
Thicket (Station B)	132
Oak forest (Station E)	123
Beech-maple forest (Station A)	100
Mesophytic ravine (Station D)	79

What this means in standardized water loss from the atmometers in the Beech-maple climax forest, is as follows:

Fuller	1910	8.1 cc average loss per day
Fuller	1911	7.4 cc average loss per day
Fuller	1912	5.6 cc average loss per day
Fuller	3 seasons	7.0 cc average loss per day
Weaver	1914	8.4 cc average loss per day
Cain and Friesner	1928	6.6 cc average loss per day

Fuller's results obtained in northern Indiana and the present results from south central Indiana are made interesting by comparison with those of Weaver (9) where he found the western climax forest, com-

posed of hemlock, cedar, etc., had a daily evaporation of 8.4 cc. This is a remarkable comparison with the eastern climax and is substantiated by the vegetational form. It is also worthy of note that the oak forests for northern Indiana and the present work also show a close relation. So, as Fuller has suggested, a widespread formation, as the Beech-maple climax forest, can well be used as a basis for comparison of evaporation rates. Such similarity of results gives the worker greater confidence in interpreting his data.

From the data presented in Table II, it can be seen that there are certain seasonal evaporation characteristics. In the first place, the midsummer months of July and August are decidedly equable in so far as evaporation is concerned. For instance, at Station C the least weekly evaporation is 90 cc while the greatest weekly evaporation is 112 cc during these midsummer months, a difference of 22 cc. Similarly, for Station B the greatest difference is 25 cc; Station E, 26 cc; Station A, 20 cc, and for Station D, 13 cc. In the month preceding and the month following, the weekly fluctuations are greater. In the early summer month of June we find a difference, between the week of the greatest evaporation and the week of the least evaporation, of 61 cc for Station C. Similarly, for Station B the difference is 44 cc; Station E, 52 cc; Station A, 42 cc, and Station D, 40 cc. For the early autumn month of September, the fluctuations are less consistent for the different stations. At Station C the difference is 25 cc; Station B, 60 cc; Station E, 46 cc; Station A, 47 cc, and for Station D, 23 cc.

Considering the whole season, we find the greatest difference in weekly water loss for Station C to be the difference between 56 cc and 156 cc. If these differences between weeks for the various stations are expressed in the ratio of the least loss to the greatest, we find the following: Station C = 1:3, Station B = 1:4, Station E = 1:6, Station A = 1:5, Station D = 1:9. From these ratios it would seem that the more open associations show quantitatively less fluctuations than the heavily wooded associations. The present data agree with that of Fuller in that the pioneer associations have higher evaporation rates; but the pioneer associations in the Dunes region showed quantitatively greater fluctuations, while in the Sycamore Creek region the greater fluctuations are *not* in the pioneer associations but in those more advanced. This difference may be explained by more extreme conditions for the Dunes region and by the relatively greater vegetational protection of the wooded stations over the old-field Station C.

Fuller (2) calls attention to the maximum and minimum *daily* evaporation rates for various stations in the Dunes region. For the cottonwood dune, for the midsummer seasons of 1910, 1911 and 1912, respectively, the maximum daily loss (average for one week) was 32 cc, 42 cc and 31 cc; the minimum daily average was 12 cc, 11.5 cc and 12.2 cc. In the oak forest he found the following results for the seasons of 1911 and 1912, respectively: Midsummer maximum, 17.5 cc and 10 cc; minimum of 2.7 cc for both years, and averages of 9.8 cc and 7.8 cc.

For the entire season in the Sycamore Creek region, we find comparative daily evaporation as given in Table III. The average of the daily evaporation for the entire season for each station is shown in Table II.

TABLE III, MAXIMUM AND MINIMUM DAILY EVAPORATION, 1928

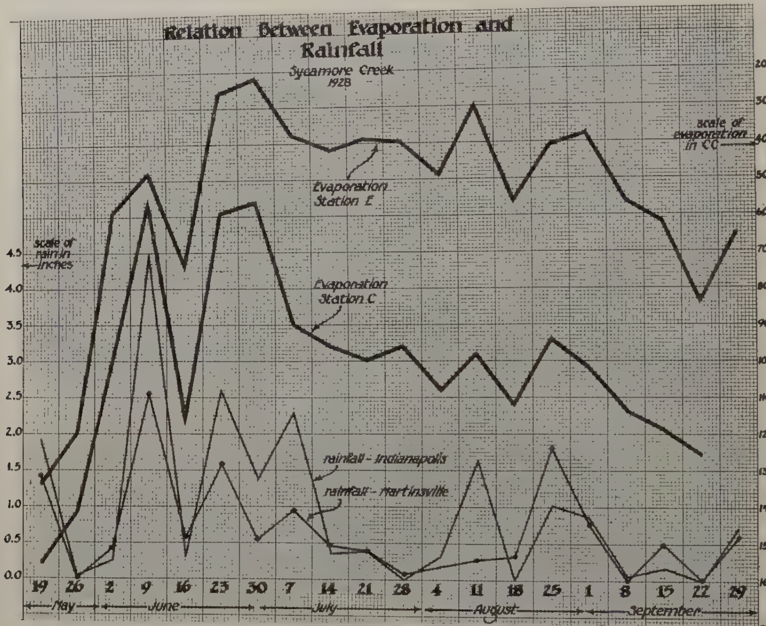
Station	Association	Maximum		Minimum		
		Amount lost	Week	Amount lost	Week	
C	Old field	22.3 cc	5-19	8.0 cc	6-9	
B	Thicket	19.3 cc	5-19	4.1 cc	9-1	
E	Oak woods	19.1 cc	5-19	3.1 cc	6-30	
A	Beech woods	14.3 cc	5-19	2.9 cc	6-30	
D	Ravine	16.3 cc	5-19	1.7 cc	6-23	

Table IV is designed to emphasize the seasonal characteristics of the evaporation rates of the different stations, on a basis of the average weekly losses for spring, early summer, midsummer and early autumn. It is readily seen that the two weeks in May, designated as spring, are conspicuous because of their greater losses. One of the important contributing factors is that the vegetation has not developed its full foliage. Although the month of June (early summer) is a period of great fluctuations, as has been shown, it is seen to average fairly close to the following periods:

TABLE IV, AVERAGE WEEKLY EVAPORATION BY SEASONS, 1928

Season	Loss from stations in cc					Average
	C	B	E	A	D	
Spring	148.5	130.0	127.5	99.0	100.0	121.0
Early summer	77.2	51.7	46.4	41.6	29.6	48.8
Mid summer	99.2	57.7	42.0	26.6	22.1	51.5
Early autumn	115.2	46.6	61.0	45.5	24.2	57.6

It does not seem possible to make a very consistent comparison between rainfall and evaporation by weekly periods. Evaporation would be expected to vary inversely with rainfall, so, in Figure 2, evaporation is plotted on an inverted scale. The high and low stations, C and E, are plotted against the rainfall for Indianapolis and Martinsville, the two closest stations. The first is about twenty-five miles northeast of the region under study, while the latter is about six miles



south. The evaporation curves parallel each other in practically all cases. Their peaks and depressions also show some correlation with those of the rainfall. They rise or fall together twelve out of twenty weeks. They show, as well, some comparison in degree of fluctuation. However, it is to be recognized that rainfall, expressed in inches by weekly periods is poor for comparative purposes. By way of illustration: Two inches of rainfall might occur within a few hours, while the remainder of the week could have a low relative humidity. Under such conditions, the weekly evaporation would be high. Another week would have two inches of rainfall scattered out in daily drizzles, with a continuously high relative humidity. During such a week the evapo-

ration would be low, and it would be futile to plot evaporation against rainfall.

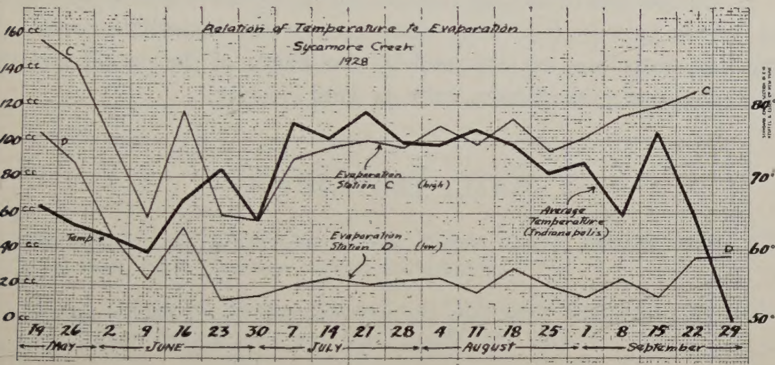


Figure 3 shows an attempt to correlate average weekly evaporation with average weekly temperature. (Indianapolis is the closest station.) There is even less apparent correlation here than there was for rainfall, since only seven out of twenty stations show any direct relation in peaks and depressions.

Data on relative humidity, air movement and length and intensity of insolation were not obtainable for the past season. Any one of these atmospheric factors is harder to obtain than the evaporating power of the air (as obtained by Livingston porous clay cup), which is the most valuable datum, since it represents a summation of all the rest.

SUMMARY

1. Atmometer stations were established in four associations typical of secondary succession in upland hardwood, namely: old-field association, thicket, oak forest and Beech-maple climax forest.

2. The highest rate of evaporation occurs in the primary stage of succession, and diminishes, in the above order, to the climax, as follows: 220: 132: 123: 100:, in which 100 (for the Beech-maple climax) equals an average daily loss of 6.61 cc.

3. The ratio of minimum to maximum weekly evaporation is lowest in the primary association, and increases, in the above order, as follows: 1:3, 1:4, 1:6, 1:5.

4. Considered on a seasonal basis for 1928, spring is characterized

by high evaporation; early summer and early autumn by considerable fluctuations, and midsummer by uniformity.

5. Comparison of average rainfall and temperature with evaporation, by weekly periods, is of little value because the immediate conditions affecting water loss are obscured by the length of the period and the intervention of other factors, such as wind velocity.

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